

THE ORDER CENTROSPERMAE¹

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ABSTRACT

Perhaps no other order of flowering plants of its size is as well investigated morphologically, ultrastructurally, and chemically as is the Centrospermae. The betalain pigment discoveries of the early 1960s were followed by the more recent discovery of unique protein depositions in the sieve-element plastids of members of this order. These and other molecular data, including DNA-RNA hybridization results, have permitted a circumscription of the order based on 11 core families, including all 9 betalain families: Aizoaceae, Amaranthaceae, Basellaceae, Cactaceae, Chenopodiaceae, Didiereaceae, Nyctaginaceae, Phytolaccaceae, and Portulacaceae, as well as two anthocyanin families: Caryophyllaceae and Molluginaceae. Several smaller betalain taxa (including *Gisekia*, *Halophytum*, *Hectorella*, and *Dysphania*) which are sometimes treated as independent families or as members of one of these 11 core families also clearly belong to the order. Other families such as the Bataceae, Gyrostemonaceae, Vivaniaceae, and Theligonaceae are excluded from the Centrospermae. The betalain evolutionary line of centrospermous families may have originated from a centrospermous ancestor which lost the ability to produce anthocyanins and then subsequently gained the two or three steps required to produce betalains. Pollen morphology of centrospermous taxa and the widespread occurrence of C₄ photosynthesis in the Centrospermae are also discussed.

Since all the review papers from a symposium on the "Evolution of Centrospermous Families," presented in July, 1975 during the XIIth International Botanical Congress, Leningrad, USSR, have now been published (Mabry & Behnke, 1976a), a summary of our current views of the Centrospermae (or Caryophyllales) will suffice in this review. This account will emphasize the way our interpretations of the order have been shaped by molecular data.

Since 1876 when Eichler (see Table 1) introduced the name for the order, the Centrospermae have always contained a core of about 8–12 families. Eichler (1876 and, in part, 1878) recognized most of what we now consider to be centrospermous families including, for example, the Cactaceae (in the 1876 treatment). In the 100 years following Eichler's work, most systematists also included those families now generally recognized on the basis of molecular data as belonging to the order but often included additional ones (compare Tables 2, 3 and 4). The molecular data which bear upon our current treatment of the order are summarized in the following sections.

SIEVE-ELEMENT PLASTIDS

Of all the modern approaches for investigating the Centrospermae, none has, in my opinion, contributed more to our understanding of the circumscription of the order than the ultrastructural investigations of the sieve-element plastids.

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TABLE 1. Centrospermae (A. W. Eichler, 1876).

I. Order: Oleraceae	III. Order: Opuntinae
1. Polygonaceae	6. Phytolaccaceae*
2. Nyctaginaceae*	7. Portulacaceae*
3. Chenopodiaceae*	8. Aizoaceae*
4. Amaranthaceae*	9. Cactaceae*
II. Order: Caryophyllinae	(? In this Order perhaps
5. Caryophyllaceae	Begoniaceae)

* Betalain families.

The discovery by Behnke that the nine core betalain families (see Table 4) as well as the two core anthocyanin families (the Caryophyllaceae and Molluginaceae) contain ringlike inclusions composed of proteinaceous filaments of a type (Fig. 1) not found elsewhere in the angiosperms (for current reviews, see Behnke, 1976a and in press) established that these eleven families represent the core centrospermous families. Behnke (in press) defined the sieve-element plastids which are unique to the Centrospermae as belonging to the P-III subtype. It is my current view that the presence of the P-III subtype sieve-element plastids in a taxon which classical data suggest might be centrospermous (see Eckardt, 1976 for comments on centrospermous characters) establishes that it belongs to the Centrospermae.

C₄ PHOTOSYNTHESIS IN THE CENTROSPERMAE

It is interesting that among the dicotyledons which have the C₄ photosynthetic pathway (the Kranz syndrome), 7 of the 11 families (Table 5) and about 85% of the genera have been reported among the Centrospermae (Walter Brown, private communication). It is perhaps significant that the Phytolaccaceae, which most workers consider to be the basal family of the order, exhibits only the C₃

TABLE 2. Caryophyllidae (Cronquist, 1968).

I. Order Caryophyllales	II. Order Batales
1. Phytolaccaceae* (incl. Achatocarpaceae, Agdestidaceae*, Barbeuiaceae, Gyrostemonaceae, Petiveriaceae*, Stegnospermaceae*)	1. Bataceae
2. Nyctaginaceae*	III. Order Polygonales
3. Didiereaceae*	1. Polygonaceae
4. Cactaceae*	IV. Order Plumbaginales
5. Aizoaceae* (incl. Mesembryanthemaceae*, Tetragoniaceae*)	1. Plumbaginaceae
6. Molluginaceae	
7. Caryophyllaceae (incl. Illecebraceae)	
8. Portulacaceae*	
9. Basellaceae*	
10. Chenopodiaceae (incl. Dysphaniaceae*, Halophytaceae*)	
11. Amaranthaceae*	

* Betalain families.

TABLE 3. Caryophyllales, Polygonales and Plumbaginales (Takhtajan, 1973).

27. Ordnung. Caryophyllales	10. Basellaceae*
1. Phytolaccaceae* (incl. Achatocarpaceae, Agdestidaceae*, Barbeuiaceae, Petiveriaceae*, Stegnospermaceae,* excl. (?) <i>Rhabdodendron</i>)	11. Didiereaceae*
2. Gyrostemonaceae	12. Halophytaceae*
3. Bataceae	13. Hectorellaceae*
4. Nyctaginaceae*	14. Caryophyllaceae (incl. Illecebraceae)
5. Molluginaceae (incl. Gisekiaceae*)	15. Vivianiaceae
6. Aizoaceae*	16. Amaranthaceae*
7. Tetragoniaceae*	17. Chenopodiaceae* (incl. Dysphaniaceae*)
8. Cactaceae*	28. Ordnung. Polygonales
9. Portulacaceae*	Polygonaceae
	29. Ordnung. Plumbaginales
	Plumbaginaceae (incl. Armeriaceae)

* Betalain families.

pathway. Although the C₄ pathway probably represents a derived condition as taxa of the order radiated into xeric and other high light intensity habitats, it is likely that some form of preadaptation for the Kranz syndrome exists throughout the order. This preadaptation has permitted repeated and independent evolution of the syndrome at various times and in numerous genera in at least seven families of the order (Walter Brown, private communication). The only other dicotyledonous families exhibiting the C₄ pathway are the Boraginaceae (*Heliotropium* in part), Compositae (7 genera), Euphorbiaceae (*Chamaesyce*), and Zygophyllaceae (3 genera).

It should also be noted that the CAM (crassulacean acid metabolism) photosynthetic pathway occurs in members of the Cactaceae and Aizoaceae; this pathway, although anatomically, functionally and phylogenetically distinct, does utilize enzymes of the Kranz syndrome. Although CAM plants are photosynthetically

TABLE 4. Order Centrospermae^a or Caryophyllales (modified here from Mabry, 1976). (Taxa with P-III subtype sieve-element plastids.)

SUBORDER CHENOPODIINEAE ^b (BETALAIN FAMILIES)	Nyctaginaceae
Aizoaceae (incl. Tetragoniaceae and possibly Gisekiaceae)	Phytolaccaceae (incl. Achatocarpaceae, Agdestidaceae, Petiveriaceae, Stegnospermaceae)
Amaranthaceae	Portulacaceae (incl. <i>Hectorella</i>)
Basellaceae	SUBORDER CARYOPHYLLINEAE (ANTHOCYANIN FAMILIES)
Cactaceae	Caryophyllaceae
Chenopodiaceae (incl. Dysphaniaceae)	Molluginaceae (excl. <i>Gisekia</i>)
Didiereaceae	
Halophytaceae	

^a Certain families which on occasion have been treated as members of the Centrospermae but are now known to contain neither the Centrospermae-specific sieve-element plastids (subtype P-III) (see Behnke, 1976a, 1976b, in press) nor betalains are excluded from the order: Polygonaceae, Plumbaginaceae, Fouquieriaceae (Behnke, 1976b), Frankeniaceae (Behnke, 1976b), *Rhabdodendron* (Behnke, 1976b; remains to be analyzed for pigments), Vivianiaceae (Behnke & Mabry, 1977), Theligonaceae (Mabry et al., 1975), and Bataceae and Gyrostemonaceae. So far neither anthocyanins nor betalains have been detected in the latter two families both of which contain glucosinolates (see Goldblatt et al., 1976 for recent comments on the status of these two families).

^b Whether or not such betalain taxa as *Petivera* and *Agdestis* (Behnke et al., 1974), *Halophytum* (Hunziker et al., 1974), *Gisekia* (Mabry, Behnke & Eifert, 1976), *Dysphania* (Mabry & Behnke, 1976b) and *Hectorella* (Mabry, preliminary results) should each be treated as families in the suborder Chenopodiineae or as members of one of the core betalain families is not resolved.

TABLE 5. Kranz and CAM Photosynthesis^a in the Order Centrospermae^b (data from Walter Brown, private communication, 1976).

Suborder Chenopodiineae (Betain Families)		Suborder Caryophyllineae (Anthocyanin Families)	
Aizoaceae	Kranz and CAM	Caryophyllaceae	Kranz
Sesuvieae	Kranz	Lychnideae	C ₃
Gisekiaceae	Kranz	Polycarpeae	Kranz (1 genus)
Tetragoniaceae	C ₃	Paronychieae	C ₃
Amaranthaceae	Kranz (11 genera)	Diantheae	C ₃
Basellaceae	C ₃ (3 genera)	Alsineae	C ₃
Cactaceae	CAM	Sperguleae	C ₃
Chenopodiaceae	Kranz (31 of 67 genera)	Molluginaceae	Kranz (2 genera)
Dysphaniaceae	C ₃		
Nyctaginaceae	Kranz (3 genera)		
Phytolaccaceae	C ₃		
Achatocarpaceae	C ₃		
Agdestidaceae	C ₃		
Petiveriaceae	C ₃		
Stegnospermaceae	C ₃		
Portulacaceae	Kranz (1 genus)		

^a Kranz = C₄ photosynthesis; CAM = crassulacean acid metabolism pathway.
^b Not yet examined: Didiereaceae, Hectorellaceae and Halophytaceae. (Added in proof: Didiereaceae and Halophytaceae are C₃.)

inefficient, they are efficient at conserving water (see, for example, Winter, 1974) since they, unlike C₃ and C₄ plants, have their stomata open only at night. In contrast, Kranz plants have probably been selected for efficient photosynthesis since they, unlike C₃ plants, have evolved an anatomy and enzymatic system which permits them to provide the Calvin cycle with high levels of CO₂ in an oxygen-deficient atmosphere. In the presence of low oxygen concentrations the enzyme which fixes CO₂ in the Calvin cycle, ribulose diphosphate carboxylase oxygenase, is free to function strictly as a carboxylase; therefore under these conditions and with high CO₂ levels and high light intensities, CO₂ fixation is apparently maximized. Thus the reasons for selection of the Kranz syndrome in the Centrospermae (and elsewhere) may be associated in part with evolution in habitats of high light intensity, which, of course, includes many of those which are xeric. Other factors such as salinity also may be important for the selection of C₄ and CAM photosynthesis. In any case, the widespread occurrence of the Kranz syndrome in both betalain and anthocyanin centrospermous families and its sporadic and limited occurrence in other dicotyledons supports current treatments of the Centrospermae (see Table 4) and provides additional evidence that the Centrospermae is an old, independent evolutionary line in the angiosperms.

PIGMENT DICHOTOMY AND DNA-RNA HYBRIDIZATION DATA
FOR CENTROSPERMOUS FAMILIES

Higher plants usually contain vacuolar red and yellow pigments which are either anthocyanins or betalains (Fig. 2); however, so far as known, the two types of pigments never occur together in the same plant or even in species

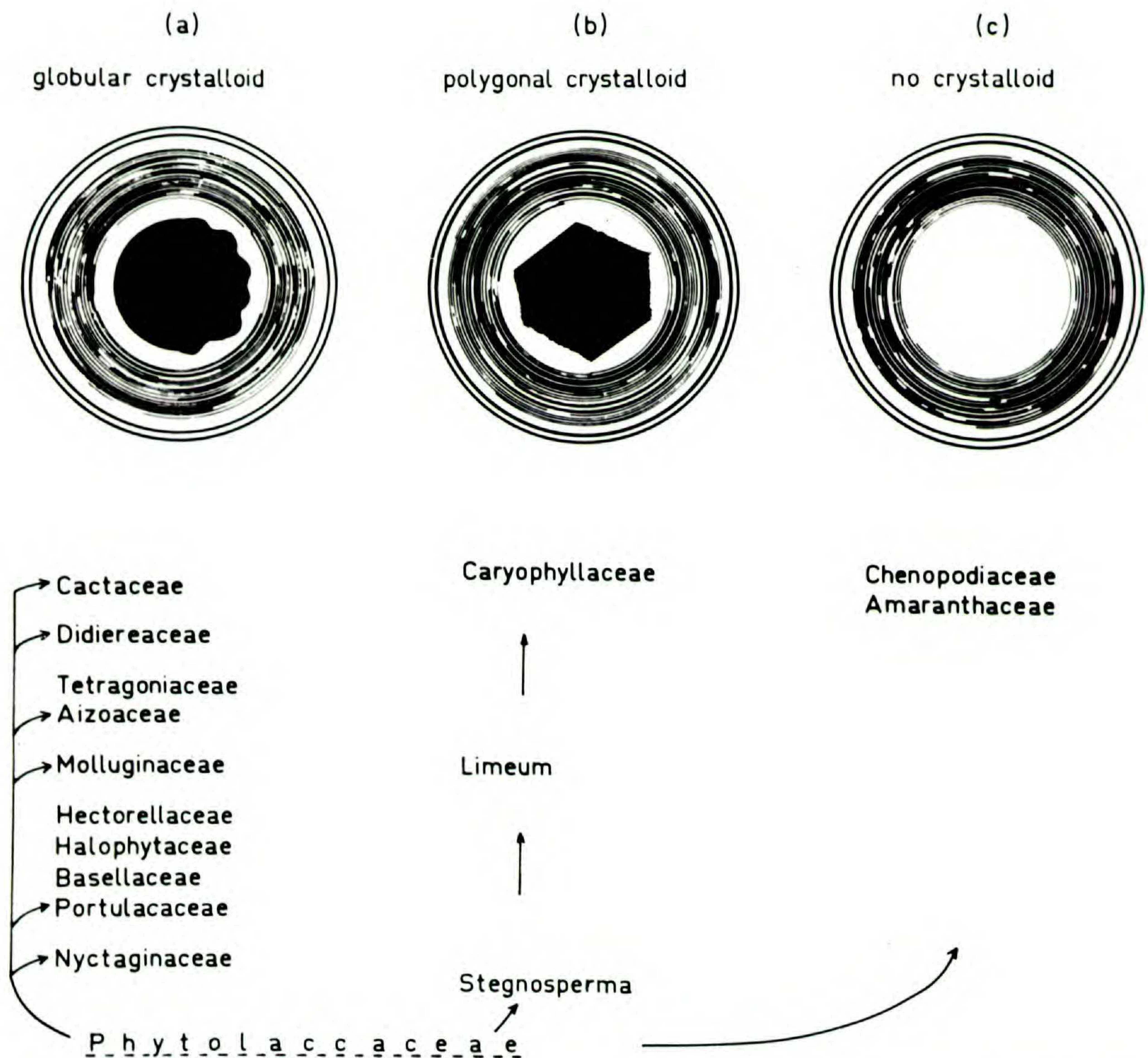


FIGURE 1. The P-III subtype sieve element plastids which are characteristic for the Centrospermae always contain a ring-shaped bundle of protein filaments with either globular (a) or polygonal (b) protein crystalloids or no crystalloid at all (c). I gratefully thank Prof. H.-D. Behnke for this figure which illustrates the distribution of these three modifications of P-III subtype in the Centrospermae.

of the same family. Of these two types, anthocyanins are much more widespread, indeed, they account for most flower pigments in higher plants (for recent reviews of anthocyanins, see Timberlake & Bridle, 1975; Harborne, 1967). In the 1960s it became clear that most centrospermous families contained an entirely new class of red and yellow pigments, designated in 1966 as the "betalains" (Mabry & Dreiding, 1968; for more current reviews, see Mabry, 1973, 1976; Mabry, Kimler & Chang, 1972; Piattelli, 1976). Although we know today that betalains also account for some of the orange and red pigments in many mushrooms, notably species of *Amanita* (Döpp & Musso, 1973, 1974; von Ardenne et al., 1974), these nitrogenous pigments have not yet been reported outside the Centrospermae among angiosperms. It is this restricted distribution of betalains as well as their being mutually exclusive with anthocyanins that makes them interesting as phylogenetic markers.

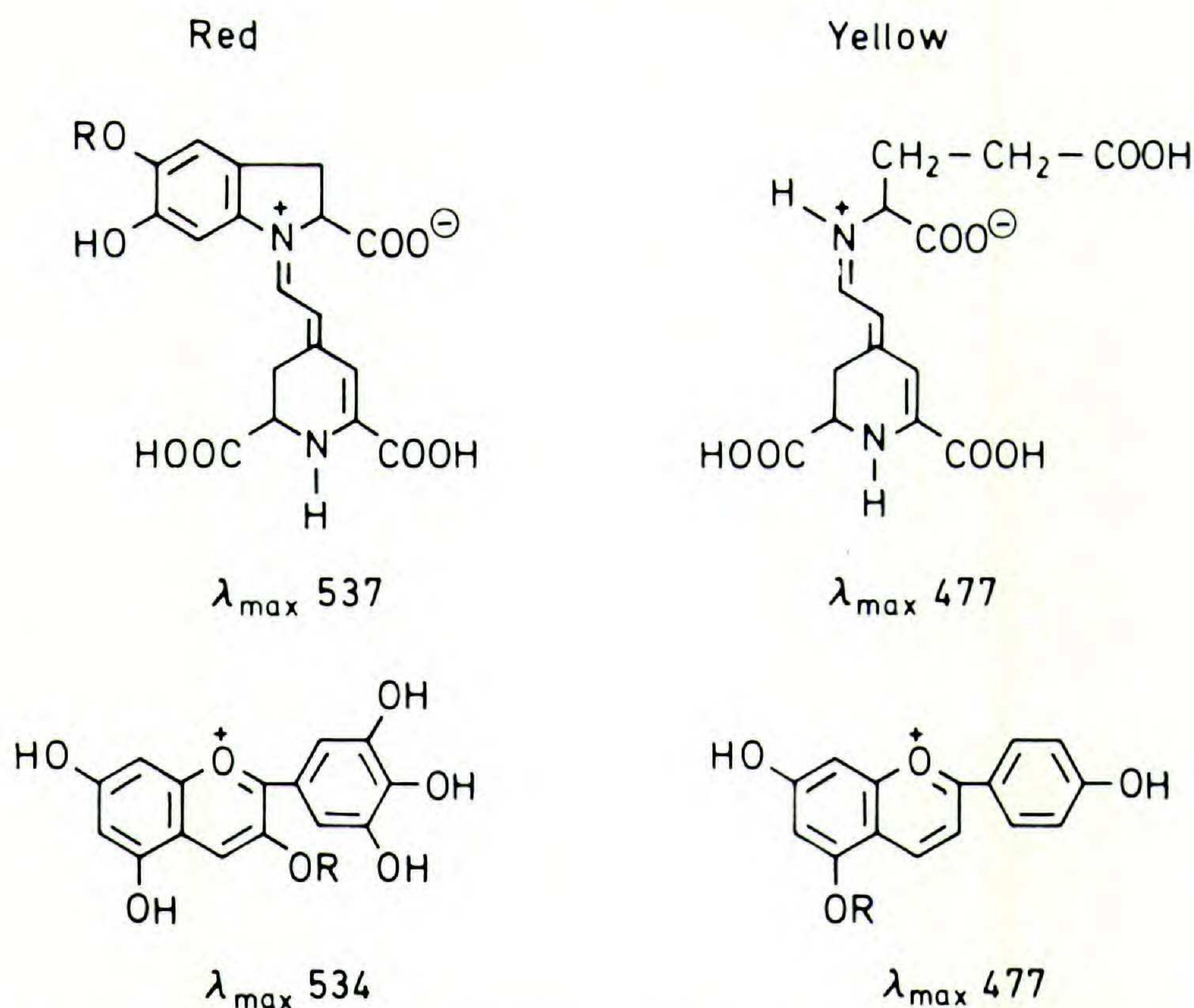


FIGURE 2. The visible absorption maxima of typical red and yellow betalains (top row), which are found only in phyletically related centrosperous families and mushrooms, are similar to those for some red and yellow anthocyanins (bottom row). Anthocyanins account for pigments in most plants, including members of two centrosperous families, the Caryophyllaceae and Molluginaceae.

BIOGENESIS OF BETALAINS

It is the biogenesis of betalamic acid and its subsequent condensation with amino acids and amines which appears to be significant among angiosperms for centrosperous plants. It now appears that the 4,5-extra diol cleavage of L-dopa (Fig. 3) can lead to betalamic acid (Fischer & Dreiding, 1972; Impellizzeri & Piattelli, 1972; Chang et al., 1974) in the Centrospermae and the mushrooms (Musso, private communication) and to stizolobic acid in the anthocyanin-containing Leguminosae (Ellis, 1976) and also mushrooms (Saito et al., 1975, 1976; Musso, private communication). Yet the conversion of the cleaved product to betalamic acid and its conversion into other betalains is known for the Centrospermae and mushrooms only. Whether or not these different groups of organisms utilize the same enzymes to synthesize betalains is not known.

PHYLOGENETIC SIGNIFICANCE OF BETALAINS

Among angiosperms, betalains are known only for centrosperous families, and we use this unique character to circumscribe the suborder Chenopodiineae, order Centrospermae (see Table 4). Whether or not all systematists accept this particular subordinal treatment is not important; it is, however, significant that today the presence of betalains in a family of angiosperms has become a key character used by all workers for its inclusion in the Centrospermae. Such families as the Cactaceae and Didiereaceae were allied with the other betalain

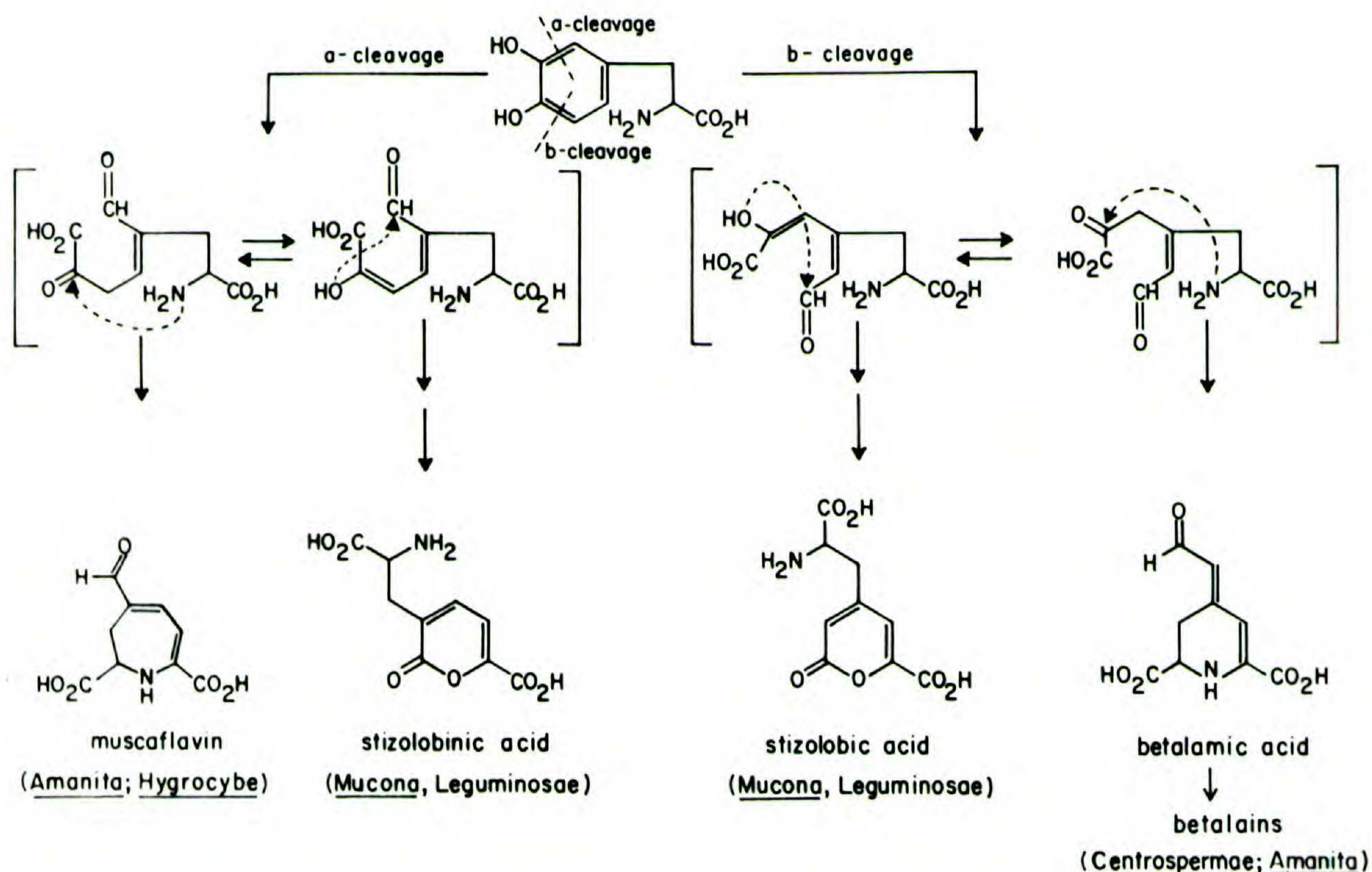


FIGURE 3. L-Dopa is known to undergo 2,3- (a-cleavage) or 4,5- (b-cleavage) extradiol cleavage in different organisms. Only in the Centrospermae and in mushrooms does L-dopa lead via the b-cleavage pathway to betalamic acid, the precursor of all other betalains. I thank Prof. H. Musso, Univ. of Karlsruhe, for private discussions which led to the scheme presented here.

families with a greater degree of confidence once their pigments were recognized. Of course, other data such as Jensen's (1965) serological results also firmly established a close relationship of the Didiereaceae to the betalain families, especially the Cactaceae and Portulacaceae.

I suppose over the years the most controversial question has focused upon our 1963 (Mabry, Taylor & Turner, 1963) proposal that the Centrospermae be reserved for the betalain families, with the closely related but anthocyanin-producing centrospermous families (e.g., Caryophyllaceae and Molluginaceae) being placed in a close but distinct order, the Caryophyllales. Although we did not then nor do we now concern ourselves with resolving the question of rank, the separation of the centrospermous families such as the Caryophyllaceae into a separate order "disturbed" a number of leading systematists. Therefore, our current treatment (Table 4), which still maintains distinct taxonomic categories (suborders) for the betalain and anthocyanin families, is more acceptable because all the families are recognized as being "centrospermous." While the phylogenetic importance of the betalains is emphasized in our current treatment, the significance of other characters is recognized. It should be noted once more that our current treatment has been sharply influenced by the occurrence of the same P-III subtype sieve-element plastids in the Caryophyllaceae and Molluginaceae as are found in the betalain families. Despite having our views shaped by different kinds of data, the views of myself and many leading systematists are converging towards a common interpretation of the Centrospermae.

TABLE 6. Pollen Morphology (Nowicke, 1975).

Taxa with Centrospermae-Specific Pollen: Spinulose and Tubuliferous/Punctate Ektexine	Some Taxa with Noncentrospermous Pollen
Betalain Families	Achatocarpaceae
Aizoaceae	Bataceae
Amaranthaceae	Gyrostemonaceae
Basellaceae	Theligonaceae
Cactaceae	Polygonaceae
Chenopodiaceae (incl. Dysphaniaceae)	
Didiereaceae	
Nyctaginaceae	
Phytolaccaceae	
Portulacaceae	
Anthocyanin Families	
Caryophyllaceae	
Molluginaceae	

A number of families sometimes treated as being centrospermous but which contain neither the P-III subtype sieve-element plastids nor betalains are now excluded from the Centrospermae proper (see Table 4, footnote a). Although the available molecular data do not suggest an alternative alignment for many of these taxa, this is not the case for the Bataceae and Gyrostemonaceae. DNA-RNA hybridization data bear upon the relationship of the Bataceae to the Centrospermae (Chang & Mabry, 1974). First, these data indicate that the betalain families which were tested are closer to each other than to any other family and that the Caryophyllaceae is the closest family to the betalain group. At the same time, the Bataceae were clearly separated from the Centrospermae on the basis of the available DNA-RNA hybridization data. Moreover, it is significant that Prof. Martin G. Ettlinger, University of Copenhagen, recently detected (unpublished manuscript) benzylglucosinolate in *Batis maritima* L., a species previously reported to contain thioglucosidase (Schraudolf et al., 1971). On the basis of these and other data, Prof. Ettlinger allies the Bataceae with other glucosinolate-containing families (Ettlinger & Kjaer, 1968); furthermore, the isolation of an isothiocyanate from *Codonocarpus cotinifolius* (Desf.) F. Muell. (Bottomley & White, 1950) indicates that the Gyrostemonaceae also belongs with these same families. As noted in the next section, the studies of pollen structure not only support a close relationship of Bataceae to the Gyrostemonaceae but also distinguish these two families from those in the Centrospermae (Goldblatt et al., 1976; Nowicke, 1975).

As a result of discussions with Prof. F. Ehrendorfer (Vienna) and from comments in a recent paper of his (1976), I agree that we must consider the possibility that the betalain families arose from an ancestral taxon which had lost the ability to produce anthocyanins. Such a process would require that the ancestor had lost the one or two enzymatic steps required to convert dihydroflavonols into anthocyanins and subsequently gained the two or three steps needed to form betalamic acid from L-dopa and then condense this aldehyde with various amines and amino acids to produce the red and yellow betalains.

POLLEN MORPHOLOGY IN THE CENTROSPERMAE

Recent investigations (Nowicke, 1975; Skvarla & Nowicke, 1976) of pollen morphology for centrospermous taxa (Table 6) also support a close relationship of the betalain families with the Caryophyllaceae and Molluginaceae in accord with our treatment (Table 4). In her examination of 190 species from 16 families by light and scanning electron microscopy, Nowicke (1975) found three common pollen types, all with a spinulose and tubuliferous/punctate ectexine among the betalain families and the Caryophyllaceae and Molluginaceae. Two additional minor related pollen types were detected in the Nyctaginaceae.

The pollen morphology of other taxa such as Achatocarpaceae, Bataceae, Gyrostemonaceae, Polygonaceae, and Theligonaceae do not support their inclusion in the Centrospermae. Of these, only the Achatocarpaceae would appear to be centrospermous on the basis of having P-III subtype sieve-element plastids; the pigment content of this taxon is not yet known.

SUMMARY

It is our view that all the betalain families and the two anthocyanin families, the Caryophyllaceae and Molluginaceae, are derived from a common "centrospermous" ancestral taxon which evolved the P-III subtype sieve-element plastids now characteristic of all these families. In addition, the ancestor was probably preadapted for C₄ photosynthesis and for a pollen morphology with spinulose and tubiferous/ektexine. The ancestral taxon for the betalain families may have arisen either from a taxon which had anthocyanins, then lost them and later gained betalains, or from a taxon which had not previously contained either type of pigment. In any case, the centrospermous evolutionary complex is now represented by eleven core families which in my opinion are best treated in one order, the Centrospermae or Caryophyllales, which consists of a betalain-suborder, the Chenopodiineae, and an anthocyanin-suborder, the Caryophyllineae (Table 4).

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